

Metagenesis as a Possible Key to Animal Form

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The origin of metazoan form is attributed to the evolutionary modification of a metagenic life cycle, a model for which is proposed, based on two alternating diploid entities, here termed *troph* and *gone*. These are expressed in the Hydrozoa and Scyphozoa in their most readily identifiable form as independent polyps and medusae. Budding of the *troph* and the strobilation of the *gone* are seen as characteristic expressions of asexual reproduction, by which means each entity replicates its own generation. The formation of the *gone* by the *troph*, however, involves a change in the nature of the unit and additional trophs can only be formed by way of a zygote. The integration of the two entities (i.e. *troph* and *gone* or *troph* and *gone* plus strobilus) is considered as the underlying cause of the development of the triploblastic and coelomate condition and the role of the 1D cell is interpreted as the '*gone* primordium'. This integration is termed *syngenean*.

Recognition of the *troph*- and *gone*-derived elements in segmented protostomes identifies the adult mandibular segment as the first primary *gone* (G1). The effects on cephalization of reduction of the *troph*, of its invasion by *gone* tissue and of use of the *troph* or *gone* mouth by the adult, are considered.

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INTRODUCTION

Metagenesis is the term for a life cycle in which an asexually reproducing (budding) generation, arising from a zygote, alternates with a sexually reproducing generation (Haeckel, 1866). In the animal kingdom, metagenesis is a phenomenon that occurs so sporadically and in so small a number of seemingly unrelated groups of lower metazoans, that little phylogenetic significance has been attached to it beyond its relevance to the phylogeny of the cnidarians. Early writers on the subject (Steenstrup, 1845; Allman, 1864; Haeckel, 1866) recognized that, in its basic form, metagenesis consisted of an alternation of a 'vegetative', 'nurse' or 'feeding' generation and a 'fruiting' or gamete-producing generation. Later, others (Strasburger, 1894; Bower, 1908) characterized the alternating generations in plants in terms of chromosome numbers and identified the initiation of the gametophyte generation with the occurrence of meiosis and, although its value as the basis for a generalization was challenged from time to time (Svedelius, 1927), its precision and convenience have led to its wide acceptance as a working hypothesis (cf. Weier *et al.*, 1974).

The discovery of apogamy in pteridophytes, although confusing the issue (Lang, 1898; Farmer and Digby, 1907), has since been attributed to certain irregular mitotic figures (Steil, 1939) and accommodated as a secondary phenomenon. Although the generations are sometimes viewed as subdivisions of a single cycle (Darlington, 1978), there can be no doubt that a vegetative (or asexually reproducing) phase is followed by a sexual phase in the life cycles of all plants.

Zoologists, confronted by alternating asexual and sexual stages in the lower invertebrates, in which the haploid cells are restricted to the gonads and gametes (Campbell, 1974), were unable to establish an equivalence between the life cycles of the lower plants and animals. Many workers, following Brooks (1886), have favoured the view that metagenesis in cnidarians is a secondary condition and discussion has centred on whether the ancestral form was polypoid or medusoid, sessile or free (Thiel, 1966; Campbell, 1974; see also Boudreaux, 1979: 17, 18).

The interpretation of animal form presented in this paper depends largely on recognition of the universality of potential polypoid and medusoid phases, or their equivalents, in that order, in the life cycles of all metazoans and it attempts to follow their separate evolutionary progress in representative types within the Metameria. It could be argued that there is room for a new approach since no comprehensive theory of the relationships between the invertebrate phyla has emerged from two recent symposia of the Systematics Association (House, 1979; Conway Morris, 1985).

In hydrozoans, the polyps, gonostyles and medusae which succeed each other as distinct morphological entities, retain continuity of the body layers as the polypoid generation buds to form the medusoid generation. Though some doubt still exists about the metagenic status of the (young) scyphopolyp and (older) scyphistoma, consensus of opinion favours a polypoid interpretation (Campbell, 1974; Thiel, 1966; Chapman, 1966). The direct transformation of the strobilating scyphistoma into ephyrae (e.g. in *Aurelia*) and the development of gonads in the lucernarian scyphopolyp (Hornell, 1893; Hyman, 1940: 509), however, demonstrate that ultimately a specific region must become medusoid in nature. In the normal process of ephyra production, the apical disc or, on occasion, the first three discs, either degenerates or resumes a polypoid existence (Thiel, 1966: 16-20). The pedal disc can also be regarded as part of the polypoid tissue, since it reverts to a typical polyp after the liberation of the last ephyra and a scyphistoma has been figured with a well-developed ring of polyp-like tentacles at the base of a stack of developing ephyrae (Agassiz, 1860). As in hydrozoans, the scyphozoan medusa is formed from a population of cells by transformation of part of the body wall. Campbell (1974) has pointed out that because of this and because of the diploid nature of the medusa as a whole, some workers feel that the polyp should be considered as a larval phase. This continuity of body layers from one 'generation' to the next would be comparable with the condition in pteridophytes if the 'gametophyte generation' had been defined to include the diploid tissue of the sporangia as well as the haploid prothallus formed from spore germination. In higher plants, the equivalent of the *gōne* generation in animals would then be found in the stamens and carpels, rather than in the haploid tissue alone. In other words, the haploid phase would represent only part of the 'gametophyte generation'. The implication of this alternative interpretation is that, whereas in the plant kingdom the sporophyte or asexual generation forms the conspicuous vegetative unit, in animals it is the sexual generation that has become dominant in body form (see below) and the analogy of the asexual polypoid phase should be sought in the pre-metamorphic 'primary marine larvae' (Jägersten, 1972) or their embryonalized equivalents.

The precocious formation of the sexual entity and the concurrent embryonic development of both phases of the life cycle offer a simple explanation for both the transformation of the vegetative polyp into part of an integrated and usually motile organism and for the increasing complexity of some tissues and organ systems. It would appear that, as in the higher plants, the identity of the two units in animals may have become progressively obscured during evolution as their tissues became more intimately associated. The relative dominance of the polypoid versus medusoid elements has subsequently contributed a fundamental though simple source of variation at the higher taxonomic levels.

THE SYNGENEAN MODEL

To challenge this concept, a new approach to morphology is proposed. In the present discussion, the anatomy of selected types is related to a series of models for which the following terminology is introduced (see Fig. 1). The term *troph* refers to the

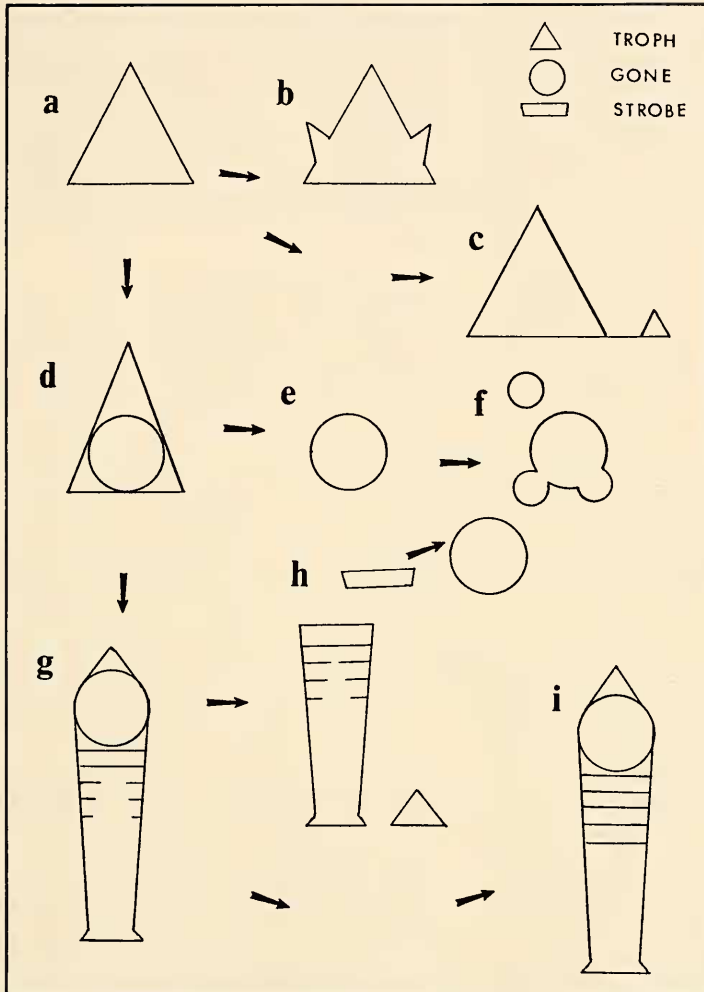


Fig. 1. Diagrammatic representation of methods of asexual reproduction. a. *Troph*. b. Asexual reproduction of *troph* by budding. c. Asexual reproduction of *troph* by alternative budding method. d. Metagenic formation of *gone* by *troph*. e. *Gone* independent of *troph*. f. Asexual production of *gonēs* by budding. g. Asexual production of *gonēs* (strobēs) by strobilation. h. Liberation and maturation of strobēs and re-settling of apical *troph*. i. Strobilated syngenean individual.

asexually reproducing, polypoid form or phase of the life cycle or to a primary larva of the trochophore (or related marine group) or to its embryonalized equivalent. The term *gone* is used for an individual of the gamete-forming, medusoid generation, or for an equivalent entity in the sexual generation of the life cycle. The term *syngenean* refers to single organisms formed by the integration of the *troph* entity with one or more *gone* entities and the term *strobilus* is used here for a segmented series and the term *strobe* refers to a single unit in the series of *gone* entities that may or may not have secondarily lost its primary reproductive function and may or may not have become tagmatized.

Hyman's (1951) rejection of the scyphistoma as a candidate for the ancestry of the Metameria was based partly on the difficulty of homologizing the head and anal

'segments' with the other body segments and partly on the assumption that 'a free-swimming animal reproducing in this manner would lose its head at each fission' (Hyman, 1951: 30). Clark's account of the corm theory (Clark, 1964: 22), like Hyman's, does not recognize a metagenic difference between the oral and pedal discs and the intervening ephyrae. Neither does it distinguish conceptually between the strobilus of a scyphistoma, the stolons of syllids, the chains of 'budding' turbellarians and the serial proglottids of cestodes. The metagenic status of each of these structures needs to be better understood because they can only be homologous if each represents the same unit or block of units.

THE COELOM AND PRIMARY GERM LAYERS

Before attempting to establish the equivalence or otherwise of these units or blocks of units, the nature of the coelom and germ layers and the position of the mouth relative to the blastopore are reconsidered. The presence of a coelom is a definitive adult characteristic of all taxa with a primary marine larva (i.e. trochophore, nauplius, actinotrocha, cyphonautes, tornaria and auricularia). By contrast, the acoelomate condition is so characteristic of the carnivorous, coprophagous or parasitic platyhelminths and nemathelminths that one must ask whether this is, in fact, the primitive condition or whether it was initially related in some way to a more advanced or symbiotic way of life.

There has been considerable interest in the method of formation of the coelom (as a schizocoel or an enterocoel) and its evolutionary origin (as a gonocoel, nephrocoel or enterocoel) (Clark, 1964). Discussion of these aspects, however, has failed to emphasize that, despite the mechanics and phylogeny of its origin, its ultimate relationship to the primary organ systems is remarkably constant. As with the formation of medusae in cnidarians, the manner of their origin may vary (contrast *Obelia* and *Aurelia*), but the results are clearly comparable.

By temporarily lessening the emphasis on the mechanism of formation in favour of its ultimate expression, we could hypothesize a situation in which a *troph* and a *gōne*, each with its own ectoderm, endoderm and mesenchyme, are integrated in such a way that the corresponding ectodermal and endodermal layers of each become confluent or intermingled. In this condition, the mesenchyme of *troph* and *gōne* would be equivalent, despite possible differences in their origin and the primary cavity within the *gōne* would be equivalent to that of the *troph* and therefore to its blastocoel. Whereas the haemocoel is recognized to be a persistent blastocoel (i.e. *troph* cavity), the coelom has not previously been considered as its counterpart in the *gōne* generation. If the *troph* and *gōne* are separate entities or the *troph* has been reduced, a cavity in the *gōne* mesenchyme will not be recognized as a coelom and an acoelomate condition will result.

Although the relationship of the three primary layers of the *troph* to their counterparts in the *gōne* unit will be influenced by the relative degree of development of each and by their physical disposition, it is to be expected that some association or co-ordination will occur between functionally equivalent units of the two generations. It will be evident that although this interpretation accepts the existence of three primary germ layers, ectoderm, endoderm and mesenchyme (including mesoderm), it modifies the concept of each by recognizing their possible dual origin. This may help explain the invasion of the annelid prostomium and its appendages by the trunk mesoderm (cf. Åkesson, 1968: 215) and the histolysis and cell migration that characterizes the pre-oral tissues of arthropods during metamorphosis (Anderson, 1966, 1973; Green, 1971; Manton, 1928), as well as the dual embryological origin and physiological control of some organ systems. Willmer's (1970) concept of the two cell-types (epithelium and mesohyl), instead of the traditional three, is equally applicable to the syngenean interpretation and reflects the

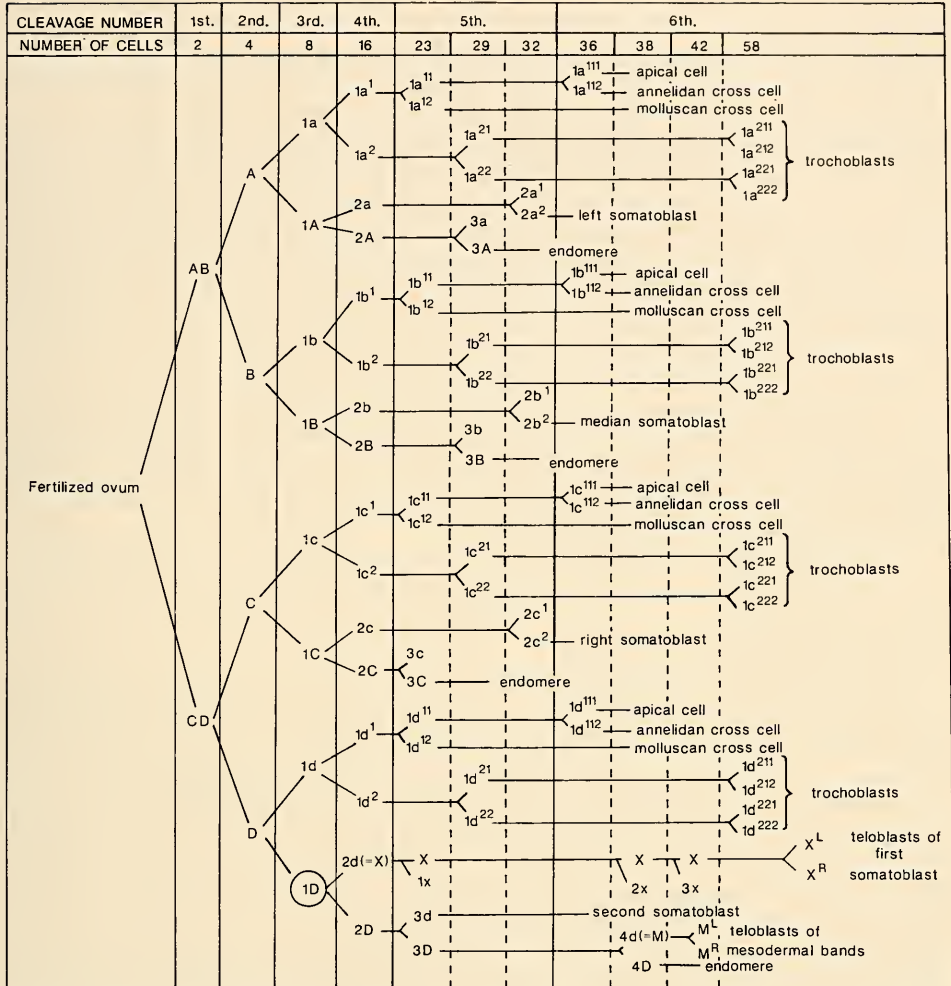


Fig. 2. Cell lineage of *Nereis* (Polychaeta) (after Okada, 1968). Note the idiosynchronous division of the 1D cell, postulated here as the *gone* primordium.

dissatisfaction with the conventional interpretation of the germ layers (Oppenheimer, 1940).

Detailed studies of embryonic cell lineages in the protostomatous phyla (Wilson, 1892; Cather, 1971; Clement, 1971; Åkesson, 1962; Kumé and Dan, 1968), which characteristically exhibit spiral cleavage, have shown that while the behaviour and fate of the A, B, C and 1d cells are comparable, that of the 1D lineage is unique (Fig. 2). Not only is the timing of its divisions unrelated to the synchrony of the other cells, but its derivatives contribute to the final structure in a unique manner. The attention that has been directed to 4d (or M), as the 'mother cell' of the mesoderm and the sex cells, has obscured the range and sum of the other 1D derivatives. In *Nereis*, 2d (=X) is the teloblast of the ectoderm of the first trunk segment and also forms the proctodaeum; 3d contributes to the posterior wall of the stomodaeum; 4d gives rise to some of the mesodermal elements of the mid-gut as well as to the mesoblast (M) with its coelom, and the 4D contributes endoderm to and behind the posterior pharyngeal region tissues. These 1D

derivatives collectively fulfil the requirements of the first medusa-equivalent (or the primary *gōne*) and succeeding units of the strobilus.

Comparison of the cell lineages of the polychaete *Nereis*, the cirripede *Mitella* and the phyllopod *Polyphemus* reveals a general similarity. From these examples, the difference between the annelid and crustacean lineages appears to be that the D lineage achieves a 'potentially self-sufficient' identity, comprising ectoderm, endoderm, mesoderm and germ cells after the third cleavage in *Nereis* (i.e. the 1D cell) (Okada, 1968) and after the second, the D^{II} (i.e. the D cell) (Shiino, 1968), in the crustaceans *Polyphemus* and *Mitella*. However, the origin of the endoblast and primordial germ cell of *Polyphemus* is comparable with *Nereis* rather than with *Mitella* (see Fig. 2), suggesting that variation in the details of cell lineage within a phylum (in this case Arthropoda) may be as great as that between related phyla.

Prior to metamorphosis, the nereid trochophore (with the exception of the 1D derivatives) can be compared with a *troph* or a coelenterate polyp which has transformed its mesogloea into mesenchyme. After metamorphosis, the original *troph* tissue is separated by the vigorous growth of the 1D derivatives, so that the pre-oral region and pygidium assume a relationship to the entire organism comparable with that of the oral and pedal regions of a scyphistoma.

Let us, therefore, consider the consequences of the proposition that the triploblastic, coelomate condition owes its origin to the development of the *gōne* (identifiable in *Nereis* as the 1D lineage, see Fig. 2) in intimate association with the *troph*, formed from the derivatives of cells A, B, C and 1d.

If each *gōne* has the metagenic status, function and anatomical potential of a medusa and the strobilus is essentially a stack of such medusae, each strobe will retain a potential self-sufficiency until this is irreversibly changed by evolution resulting in a division of labour between strobos. With progressive differentiation of a strobilus, it is to be expected that the leading units will have developed the *gōne*-orientated sensing and feeding systems to a greater degree than those following. By recognizing the first post-metamorphic (i.e. the most anterior trunk or jaw-bearing) segment in *Nereis* as G1 (see Table 1), the dual origin of the adult mouth and pharynx becomes clear. The cephalization of G2 and G3 in arthropods makes the evolution of more specialized mouth parts possible. The doubt that surrounds the homology of the peristomium in polychaetes (Schroeder and Hermans, 1975) is largely due to conflicting definitions. These doubts can be resolved, in part, by recognizing the errant polychaetes to be annelids with a well-developed and persistent *troph* and the sedentarians to be forms in which the *troph* is reduced. The role of the peristomium as the sensory and oral region of G1 (cf. the manubrium of the first medusa) is supported by the definition of Schroeder and Hermans (1975) and by embryological evidence. The peristomial appendages, together with the sub-oesophageal ganglion and invasive mesohyl which supplements the pre-metamorphic and pre-oral structures, can be regarded as elements of the first or primary *gōne*. The reciprocal growth of axons to and from the supra- and sub-oesophageal ganglia also support the concept of this *gōne* actively establishing operational partnership with the *troph* (cf. Henry, 1947).

Once the positional and functional relationships between *troph* and *gōne* are recognized, it becomes possible to interpret the proto- and deuterostomatous conditions, irrespective of assumed phylogenetic relationships. This will be deferred, however, until certain aspects of segmentation, stolonization and tagmatization have been considered.

SEGMENTATION, TAGMATIZATION AND STOLONIZATION

The segmentation of annelids and arthropods is almost ubiquitous and widely

regarded to be a primitive feature of both groups. Its partial obliteration in some arthropods may occur during maturation, as in the parasitic crustaceans, or during the embryonic stages, as in the acarine and araneid arachnids. In all these cases, the lack of segmentation is clearly secondary. Tagmatization usually accompanies and possibly precedes a loss of segmentation. It is characteristic of a specific functional specialization such as feeding, locomotion or reproduction, the obliteration of segmentation being commonly associated with the reproductive region of the body.

There is much variation and some uncertainty about the precise origin of the germ cells in the various arthropod taxa. They have been found in representative polychaetes, crustaceans and insects in all segments of the strobilus, including the mandibular (G1), but not in the pre-oral or caudal 'segments' (Green, 1971; Anderson, 1973; Snodgrass, 1935; Bitsch, 1973). Because these exceptions coincide with the postulated *troph* tissues, it is concluded that the *gōne* or the strobilus itself is the potentially fertile unit and that evolution has favoured the migration of the germ cells to restricted regions or metameres, usually those posterior to the stomach and digestive glands. Variability in the position of the genital ducts in the lower crustaceans and, therefore, in the extent of the fertile (cephalo-) thorax, contrasts sharply with the rigid patterns that characterize the malacostracans, insects, myriapods and chelicerates. In the oligochaetes, the sterile region posterior to the fertile tagma is usually reduced or secondarily modified.

TABLE 1

Segmental equivalence of the anterior appendages of the Metameria based on the syngenean interpretation of animal form

SYNGENEAN UNIT	ANNELIDA		ARTHROPODA				
	POLYCHAETA		CRUSTACEA		INSECTA		ARACHNIDA
T 1	} PHOSTOMIAL TENTACLES AND PALPS		ANTENNULES		—		—
T 2			ANTENNAE		ANTENNAE		—
T 3			LARVAL MANDIBLES	INTERCALARY SEGMENT		—	
G 1	} PERISTOMIAL TENTACLES AND PHARYNGEAL JAWS APPENDAGES OF TRUNK SEGMENTS ↓		ADULT MANDIBLES		ADULT MANDIBLES		CHELICERAE
G 2		2nd.	FIRST MAXILLA	FIRST MAXILLA		PEDIPALPS	
G 3		3rd.	SECOND MAXILLA	SECOND MAXILLA		1st. } PROSOMAL (WALKING) LEGS	
G 4		4th.	1st. } WALKING LEGS (OR MAXILLIPEDS)	1st. } THORACIC LEGS		2nd. }	
G 5		5th.		2nd. }		3rd. }	
G 6		6th.		3rd. }		4th. }	
G 7		etc.	etc.	etc.			

T: *troph*; G: *gōne*

By identifying, as the essential feature of the onset of metamorphosis in crustaceans, the simultaneous histolysis of the pre-oral musculature of the nauplius, its replacement by invasive somitic mesoderm and the development of the *adult* elements of the mandibular segment, the nauplius can serve as a point of reference for the morphogenesis of the adult jaw-bearing segment of both annelids and the egg-nauplius. The entity G1 (or the 'primary *gōne*') and the subsequent strobos (G2, G3 etc.) can then be identified and their tagmatization compared without the necessity for establishing homology of the pre-oral tagmata. The advantages of this are evident in interpreting the homologies of tagmata in arachnids and onychophorans where pre-oral (or *troph*-equivalent) structures appear to be reduced.

By adopting the nauplius in preference to the trochophore as a 'standard' or reference for the fully-developed 'primary larva' of the protostomatous phyla, the three paired appendages (antennules, antennae and *larval* mandibles), together with the proto-, deuto- and trito-cerebra, the larval eyes and the larval alimentary system (stomodaeum, larval stomach and digestive glands and the anterolateral region of the adult pharynx), can be identified as parts of the mature *troph*. In Crustacea, the replacement of larval by adult appendage musculature, like the development of pharyngeal jaws in the first trunk segment of polychaetes, is due to the activity of cells derived from the mesodermal teloblasts and ultimately to the 1D lineage (cf. Manton, 1928; Green, 1971; Anderson, 1973).

The pharyngeal region of annelids and the (adult) mandibular segment of crustaceans appear to be structures of dual origin, derived in part from the *troph* and in part from the *gone*, the development of each component varying with the taxon, but those of the *gone* invariably developing after those of the *troph*.

In insects, the intercalary segment, now widely accepted as being innervated by the tritocerebrum (Bitsch, 1973; Rempel, 1975) would, by the same reasoning, be part of the *troph* and the equivalent of the larval mandibular region of a nauplius. In the holometabolous insects, it seems to be the sudden burst of growth of *gone* tissue, initially and precociously formed during the early embryonic period, but latent during the secondary larval ('caterpillar') stage, which causes metamorphosis by completing the differentiation of each strobe and by modifying and replacing some of the *troph*'s characteristic structures — e.g. the larval eye spots and simple pre-oral appendages. In the mosquito, for example, the larval feeding brushes are replaced at metamorphosis by the highly specialized structures that form the feeding mandibles. In orthopterans, cells derived from a mesodermal somite migrate into the rudimentary antennae and proliferate to form the segmented adult antennae (Wheeler, 1893: 111). Although the 1D cell is not identifiable as such in insects, the somitic mesoderm clearly belongs to the strobilus. As such, it can be interpreted as another instance of the integration of equivalent tissues of the two generations to form a single functional structure. Although the spiral cleavage and, therefore, the possibility of recognizing the 1D lineage is replaced by superficial cleavage in the peracaridean crustaceans and the insects, there seems to be no reason to doubt the homology of the mandibular and strobilar regions of either group with their counterparts in the lower crustaceans if the adult mandibular segment is G1 in all cases. Here again, we see that although the details of differentiation may differ, the results are closely comparable because no one doubts the homology of isopod structures with their counterparts in other crustaceans.

Table 1 shows the strobilar patterns of certain metameric invertebrates, using the post-metamorphic mandibular segment as the critical means of identifying G1. This homology has not previously been justified because of the difference in form between the pre-oral appendages of the major groups. Once the pre-metamorphic appendages are recognized as the homologues of the peri-oral tentacles of a *troph*, their initial radial symmetry can be seen as secondarily modified to a paired bilateral arrangement. This change in symmetry is best understood in relation to the establishment of the antero-posterior axis of the typical syngenean metazoan, the establishment of a composite mouth and increased 'streamlining' of the head.

A reduction of the *troph* appears to have occurred within most of the major phyla during their early evolution and has possibly been a significant factor affecting variation at class level and above. The scyphozoan coelenterates, the tubicolous polychaetes, oligochaetes and hirudinean annelids as well as the chelicerate arthropods exemplify the dominance of the *gone* within the larger taxa. In segmented forms, this results in greater prominence of the derivatives of the first strobe in the pre-oral tissues and of the first two or three strobes in the composition of the mouth and gnathocephalon.

The development of multi-segmental blocks, or epitokal 'stolons' in some annelids, particularly syllids, though regarded by some earlier writers as a kind of alternation of generations (cf. Potts, 1911), is now more widely interpreted as a form of regeneration. Okada (1934) and Berrill (1952) have described the development of a new prostomium as part of the stolon head and the regeneration of a typical head when the anterior segments are amputated. At first sight, this suggests the replacement of *troph* tissue by *gōne* tissue. However, the formation of the new head blastema is closely linked with the arrival of multipotent neoblasts, formed as 'syncytial nests of small mesenchyme cells' (Berrill, 1952: 414), lying in the angles of the septum and nerve cord. If the neoblasts arise directly from the larval mesenchyme or if ectoderm derived from A, B, C or 1d lineages (e.g. 2a², 2b², 2c² — the right, median and left somatoblasts respectively: cf. Fig. 2) contributes to the new head, there is no departure from the principle of head formation from *troph*-derived tissue. The development of epitokal heads in certain polychaetes may, therefore, be a consequence of the distribution of *troph* tissue in the adult worm.

Experimental studies (Wada, 1968; Clement, 1962) have shown that embryos of protostome larvae cannot undergo metamorphosis without the D cell. However, the D cell alone, although capable of producing a 'normal' post-trochal region, dies before it can reach the stage of metamorphosis, suggesting that a normally-functioning *troph* is necessary for the development of the *gōne*.

PROTOSTOMATOUS AND DEUTEROSTOMATOUS TAXA

Grobben (1908) and some later authors (e.g. Beklemishev, 1969) have used the method of mouth formation, *inter alia*, to distinguish what they believe to be two major, fundamentally divergent stocks of metazoans: the Deuterostomia and the Protostomia. Neither group, however, has been universally accepted. For example, the validity of the deuterostomes has been under challenge in recent years (Brien, 1974; Løvtrup, 1975) and some undoubted protostomes (e.g. onychophorans; Manton, 1949) have been shown to possess a mouth that arises *de novo* and not from the blastopore or its point of closure. There seems little doubt, however, that the annelid-arthropod-mollusc-turbellarian group does possess features that indicate a true relationship between them.

The syngenean interpretation offers a solution to the dilemma about homology in regarding the mouth of the polyp in the cnidarians to be the equivalent of the mouth of the *troph* in protostomatous metazoans. The Protostomia are then seen to be a group of phyla in which the *troph* mouth remains as part of the functional adult mouth, however formed. Any exceptions to this among protostomes can be accommodated as specializations comparable with the degree of variation in cnidarian gastrulation (i.e. by epiboly, ingression or delamination). The deuterostomes, collectively identified more by the absence of protostome features, lack the homogeneity of the protostomes and appear in most, if not all, cases to be taxa in which the distinctive features of the *troph* are reduced and the oral aperture of the *gōne* becomes the functional mouth.

In these deuterostomes, where the adult mouth arises independently of the blastopore, the way in which the mouth originates lends itself to the interpretation that it is derived from the *gōne* while the blastopore is largely confined to the pygidial area. In such cases, the *troph* is still able to contribute to the sensory and neural structures of the head or lophophore. The extent to which it does so is an expression of the relative contributions of *troph* and *gōne* to the adult body form and appears to provide a simple explanation for some of the differences that exist between the 'lophophorate deuterostomes' and the 'true deuterostomes'. Close relationship between these groups would not have to be assumed in order to explain their embryological similarities.

CONCLUSIONS AND SUMMARY

If the Metazoa evolved from the Protista (Sleigh, 1979: 50-52), there is reason to argue that because metagenesis is so widespread in the Protista and Cnidaria, it could well be a fundamental characteristic of the Metazoa. In an *a priori* interpretation of metagenesis in the metazoans, the more primitive form is the free *troph* (larva) while the embryonalized equivalent (e.g. the egg-nauplius; Shiino, 1968) is its phylogenetic successor. The general trend appears to have been towards direct development, the precocious formation of the *gōne* (sexual generation) and the syngenean state. A hypogenic interpretation of the life cycle, on the other hand, offers no basis for seeking an evolutionary progression from alternating generations towards the development of primary larvae and thence to progressive embryonalization and permits the marine primary larvae to be considered as a series of individual late adaptations.

When the metagenic model is applied to the higher invertebrates, the existence and metamorphosis of the marine primary larvae become explicable without need to identify the direct or hypothetical ancestors. The introduction of the concept of *troph* and *gōne*, as models for the polyp and medusa equivalents respectively, also allows the two forms to be considered as homologues each capable of their own maturity, modifications and evolution. It also suggests that through integration they could form a syngenean animal, the morphology of which would vary depending on the relative contributions made by the *troph* and *gōne* components. The degree of development and persistence of each entity controls such features as the degree of cephalization, the presence or absence of a coelom, segmentation and tagmatization, as well as the type of mouth development. By this *a priori* approach and the avoidance of traditional assumptions, an alternative interpretation of animal form can now be offered.

The recognition of metagenesis and the almost simultaneous and integrated development of the two generations can explain the trend toward embryonalization of the larval form as an evolutionary advance. By recognizing the contribution which the *troph* and *gōne* entities each make to the functional morphology of the adult, it is possible to trace an increasing specialization of the *troph*'s sensory role in the developing brain and its decreasing role in food uptake and locomotion. Against this background, other functional systems can be isolated in similar fashion by embryological criteria and the direction of any progressive morphological series can be determined independently of existing theories about phylogeny.

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NOTE ADDED IN PROOF

'Tagmatization' is used here to describe the progressive differentiation of a block of strobcs into a tagma. It is distinct from tagmosis, in which the *troph* may be incorporated with *gōne* units, as in cephalization.

'Embryonalization' is defined as the gradual suppression of the free-living primary marine larvae (the *troph* generation) and the modification or loss of their morphological identity due to the precocious development of the *gōne* before hatching. This requires recognition of a distinction between larval (*troph*) ectoderm, endoderm and mesenchyme and the *gōne*-derived ectoderm, endoderm and mesoderm. Its range is exemplified in crustaceans where hatching may occur at any stage from a nauplius to a miniature adult. The word is identified with the syngenean interpretation of animal form and is suggested as the 'unknown force' or 'adult pressure' which lies behind adulation and acceleration as discussed by Jägersten (1972: 6, 218).